THE FAMILY ANEURACEAE IN AUSTRALIA AND NEW GUINEA: I. THE GENUS *ANEURA*

H. J. Hewson
*School of Biological Sciences, University of Sydney**

(Plates XI–XII and 3 Text-figures)

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Synopsis

Seven new species and two new varieties of an eighth species are described. The separation of the genus *Aneura* Dum. from the genus *Riccardia* Gray *sens. lat.* is analysed. Some of the distinguishing features have been modified. An attempt is made to classify the eight species into the two subgenera *Aneura* Dum. and *Lobatiriccardia* Miz. et Hatt. Several of the diagnostic characters are shown to be ineffective. Keys are provided to the species studied which are found in Australia and in New Guinea.

Introduction

It is generally recognized in the Hepaticae that the basic haploid chromosome number in any given family is stable. The previous records for Aneuraceae indicate a stable basic haploid number of ten. However, a species from the family Aneuraceae, found near Sydney, was discovered to have a basic haploid number of eight. This seemed to provide an interesting problem. However, it rapidly became evident that the taxonomy of the family was very critical in Australia and New Guinea and required sorting out before the cytology could be interpreted.

The first species of the Aneuraceae to be described from Australia was *Riccardia crassa* (sub *Jungermannia*) by Schwägrichen in 1814. Linnaeus (1753) provided the first legitimate names of members of the family, namely the European *Jungermannia pinguis* L., and *J. multifida* L. However, since they are clearly not *Jungermanniae,* S. F. Gray (1821) provided the first available generic name for members of this family. He described the genus *Riccardius* with *R. multifidus, R. pinguis,* and *R. dichotomus.*

In 1869, Carrington proposed that *Riccardius* was an orthographic error but he did not publish the correct spelling. However, in 1874 Trevisan changed the spelling to *Riccardia. R. multifida* is accepted as the lectotype.

In 1961 in the International Code of Nomenclature, *Riccardia* Gray corr. Trevisan was conserved. Thus it would seem that there is no basis for *Riccardia* Gray corr. Trevisan being called a Nomen Rejiciendum in the Index Hepaticarum (Bonner, 1962).

In 1822, Dumortier described the genus *Aneura* with the species *A. multifida, A. pinguis, A. sinuata,* and *A. palmata.* Despite the fact that *Riccardia* has priority over *Aneura* the latter name has been used extensively for the combined genera. Stephani in his Species Hepaticarum used it and was responsible for the bulk of species descriptions for Australia and New Guinea.

In the following decades there were several other illegitimate taxonomic synonyms created (see Generic Description). There also were several attempts to subdivide the genus *Riccardia sens. lat.* (then commonly known as *"Aneura"*).

* Present address: Botany Dept., School of General Studies, A.N.U., Canberra, A.C.T

In 1831, Dumortier divided his genus *Aneura* (including *Riccardia*) into two sections:

1. *Phymatia* Dum. (*A. multifida* (L.) Dum. and *A. palmata* (Hedw.) Dum. *A. multifida* is herewith accepted as the lectotype of *Phymatia*).

2. *Aneurotypus* Dum. (*A. pinguis* (L.) Dum. which is herewith accepted as the lectotype species of *Aneura*).

In 1867, Gottsche divided the genus *Aneura* Dum. (including *Riccardia*) into two genera:

1. *Aneura* Dum. (*A. pinguis* (L.) Dum. and *A. palmata* (Hedw.) Dum.).

2. *Pseudoneura* Gottsche. (*P. multifida* (L.) Gottsche, *P. humilis* Gottsche and *P. pöeppigiana* Gottsche. *P. multifida* (L.) Gottsche is herewith accepted as the lectotype of *Pseudoneura*). But *Pseudoneura* is therefore a later taxonomic synonym of *Riccardia* Gray.

Schiffner in Engler and Prantl (1893) divided the genus *Riccardia* Gray *sens. lat.* into three sections:

1. *Spinella* Schiffner et Gottsche (*R. spinulifera* Mass. = *S. magellanica* Schiffner et Gottsche—holotype).

2. *Aneura* Dum. (*Phymatia* Dum. and *Aneurotypus* Dum.).

3. *Acrostolia* Dum. (*Pseudoneura* Gottsche. *Acrostolia* is superflous since *Pseudoneura* was given as a synonym in the original publication).

The holotype of section *Spinella* is *Riccardia magellanica* (Schiffner et Gottsche) which is characterized by unique epidermal projections. This section is not known to be represented in Australia and New Guinea and consequently is not considered in this treatment.

In 1933, Malmborg segregated the genus *Cryptothallus* from *Riccardia* Gray *sens. lat.* This is a characteristic subterranean plant and the genus is accepted. However it has not been found in Australia.

In 1957, Mizutani and Hattori divided the genus *Riccardia* Gray *sens. lat.* into three subgenera:

1. *Trichostylium* (Corda) Miz. et Hatt. (*R. pinguis* (L.) Gray—holotype).

2. *Lobatiriccardia* Miz. et Hatt. (*R. lobata* Schiffner—holotype).

3. *Riccardia* Gray (*R. multifida* (L.) Gray—holotype).

In 1958, Schuster combined the two subgenera *Trichostylium* and *Lobatiriccardia* to form a new genus *Trichostylium*. The type species of *Trichostylium* is also that of *Aneura* and it is therefore a taxonomic synonym of *Aneura* (Grolle, 1960).

In 1963, Schuster divided the genus *Riccardia sens. str.* into two subgenera:

1. *Riccardia* Gray (*R. multifida* (L.) Gray).

2. *Phycaneura* Schust. (*R. reducta* Schust.—holotype).

In 1964, Schuster described a third subgenus:

3. *Anomaneura* Schust. (*R. cochleata* (Hook.f. et Tayl.) Kuntze—holotype). The two new subgenera are based on Australian species. He also recognized the two subgenera of *Aneura* described by Mizutani and Hattori:

1. *Aneura* Dum. (*A. pinguis* (L.) Dum. = *Riccardia* Gray subgenus *Trichostylium* (Corda) Miz. et Hatt.).

2. *Lobatiriccardia* Miz. et Hatt. (*A. lobata* (Schiffn.) Steph. = *Riccardia* Gray subgenus *Lobatiriccardia* Miz. et Hatt.).

Meanwhile these taxa were included in the family Jungermanniaceae until 1910. In 1838, Nees ab Esenbeck attempted classification within the

Order Jungermanniales *sens. lat.* and circumscribed a Grade Aneurae with *Aneura pinguis, A. pinnatifida, A. multifida, A. palmata* and *Trichostylium affine.* It is questionable that he intended this to circumscribe the "natural order" or Family. It was not until 1910, when Cavers described it, that the family Aneuraceae, as we know it, was effectively named and circumscribed.

Since 1814 fifty species have been recorded as occurring in Australia and New Guinea. The initial problem was to decide whether these species included both *Riccardia sens. str.* and *Aneura,* and if so, whether the distinguishing characters supported or otherwise the decision to elevate *Aneura* to generic status.

In summary see Table 1 for the distinguishing characters.

TABLE 1
Characters of Riccardia *and* Aneura

Character	*Riccardia*		*Aneura*	
	Schuster	This Treatment	Schuster	This Treatment
1. Width of thallus ..	—	(0·05) 0·5–2 (4) mm.	—	(1·5) 2–6 (12) mm.
2. Branching	1–3 pinnate	(1) 2–4 pinnate	—	1–2 pinnate
3. Gemmae	Endogenous	Endogenous	Unknown	Unknown (? exog.)
4. Oil body number ..	0–1 few/cell	0–15 per cell	(3–5) 6–40+	1–40+/cell
5. Oil body size ..	Large	2×3–12×150μ	Small	1·5×2–15×20μ
6. ♀ branches ..	On lat. branch	Lat. vent.-lat.	Ventral	Rarely lat.
7. Seta	12–16+ 4 cells	4 cells diam.	Massive	8–16 cells diam.
8. Capsule wall anatomy	—	*Riccardia*-type	—	*Trichostylium* or *Lobatiriccardia*-type

Aneura has a thallus which is more massive but less freely branched than *Riccardia.* It probably does not produce endogenous gemmae and usually carries smaller oil bodies than *Riccardia.* It has a massive seta (Fig. 2) and a capsule wall anatomy different from that of *Riccardia.*

Thus, there are two discrete definable sporophyte characters (7 and 8) separating the taxa and a number of correlated (though not so clearly discrete) vegetative characters (1–6) which support these two sporophyte characters. Since the discrete characters are structural differences and will probably be supported by the rather negative character of production versus non-production of gemmae, I have accepted them and it seems reasonable to distinguish the two genera as separate.

The Subgeneric Classification of *Aneura*

The subgeneric classification of the genus *Aneura* Dum. into the two subgenera, *Aneura* and *Lobatiriccardia* is based on thallus size, oil bodies, seta size, capsule wall anatomy and spore size.

In this work I have treated eight species, seven of which are new. There are two new varieties for the eighth species which also occurs in New Zealand. Using these species an attempt has been made to classify them into the subgenera as circumscribed by Mizutani and Hattori (1957) (see Table 2).

The result is that some of the distinctions appear inadequate. The Australian and New Guinea species include intermediates which overlap the classes. Hence, thallus size, seta diameter and spore size are ineffective diagnostic characters. On the other hand the classes for oil body size and

TABLE 2

Subgeneric Classification after Mizutani and Hattori (1957)

Subgenera and Species	Thallus Size			Oil Bodies		Seta	Capsule Wall Anatomy		Spores	
	Length cm.	Width mm.	Thickness Cells	Number per Cell	Size μ	Diameter Cells	Outer	Inner	Diameter μ	Ornamentation
Aneura										
Trichostylium (A)	—	5–10	10–15	10–40+	1·5×2·5–3×5	8–12	ad and abaxial	ad and abaxial	20–25	—
Lobatiriccardia (L)	—	3–6 (7)	+/− thinner	(3–5) 6–12	5–6×7·5 to 8–15×10–20	12+	adaxial	often both both (ad) and abaxial (i)	12–19	—
A. eachamensis ..	1–3	(1·5) 2–3 (5) L	(7) 9–10 (12) L	?	?	8 A	ad and abaxial A	ad and abaxial A	14–22 between	minutely sculptured-pilate
A. cerebrata ..	1–2 (3)	(1·5) 2–5 (10) between	15–20 (30) A	20–30 A	2×3–5×8 A	10 A	ad and abaxial A	ad and abaxial A	10–17 L	projections-papillate
A. alterniloba var. *gigantea*	(2) 3–6 (8)	(2) 4–6 (8) L	(5) 7–10 (12) L	(1) 2–5 (8) L	5×8–15×20 L	12–15 L	adaxial L	ad and (abaxial) (iii) L	14–19 L	minutely sculptured-scabrate
A. alterniloba var. *robusta*	(2) 3–5 (6)	(2) 3–6 (10) between	(6) 8–12 (15) between	1–3 L	3×3–8×15 L	11–14 between	adaxial L	ad and (abaxial) (iii) L	17–21 between	minutely sculptured-scabrate
A. athertonensis ..	2–3 (5)	2–4 L	(7) 8–10 (12) L	1–4 L	8×15–10×18 L	11–12 A	adaxial L	ad and (abaxial) (iii) L	10–15 L	minutely sculptured-scabrate
A. rodwayi ..	(1) 2–3 (4)	(2) 3–5 (10) between	10–20 (25) A	?	?	13–15 L	?	?	?	?
A. novaguineensis	(1) 2–4 (5)	(1·5) 3–5 (12) between	(7) 10–15 (20) A	?	?	16 L	?	?	?	?
A. giangena ..	2–3	2–6 L	8–12 between	?	?	?	?	?	?	?
A. kaguaensis ..	1–3	3–4 L	7–10 L	?	?	?	?	?	?	?

number, and capsule wall anatomy are discrete. If one accepts these characters as being adequate to retain the subgeneric classification, then *A. cachamensis* and *A. cerebrata* are in the subgenus *Aneura,* and *A. alterniloba* and *A. athertonensis* are in the subgenus *Lobatiriccardia.* The last four species, *A. rodwayi, A. novaguineensis, A. giangena,* and *A. kaguaensis,* cannot be classified for want of study of their oil bodies and capsule wall anatomy.

If, however, one does not accept these characters as adequate to retain subgeneric classification, further attempts to erect subgeneric taxa should wait until a complete generic monograph is available.

General Analysis and Definitions of Terms used in Classification and Description

Thallus: The external morphology of the gametophyte of *Aneura* was found to be very variable within and between localities, and within and between seasons. The range of variation within and the degree of overlap between species is sufficient to render the gametophyte of very little taxonomic value.

(i) Texture and Colour: All species have a waxy texture. The colour, however, is variable in intensity of green and this seems to be correlated with habitat, substrate and age.

(ii) Size: The thalli of all species are massive and fleshy and the classes for width and thickness as circumscribed by Mizutani and Hattori are overlapped by several species (Table 2).

(iii) Transverse Section Shape: All species are plano-convex to concavo-convex with recurved margins. However, *A. cerebrata* and *A. rodwayi* are usually very deeply concave so that the margins have a vertical orientation (Fig. 1).

(iv) Margin: The margins may be obtuse, acute or winged (see Part II). They may also be uniform or dentate. Dentition is the tendency for the margin to produce scalelike or toothlike projections. This is not found in all species, but where it is found is much more pronounced in female thalli.

(v) Apex, Mucilage papillae and Rhizoids: The apices are usually deeply dissected as a result of rapid lateral growth immediately behind the apex. *A. kaguaensis,* however, does not have a markedly dissected apex because growth is almost uniform behind and lateral to the apex.

All have ventral, non-persistent mucilage papillae, and all have ventral rhizoids. No dorsal rhizoids were observed in this genus.

(vi) Branching: All species have at least two types of branching. The first type is simply an irregular pinnate branching arising from an apparent dichotomy of the apical cell; this does not result in limited growth. The second type is usually the formation of regular alternate lobes of limited growth (i.e. bipinnate).

The most distinctive phenomenon observed in branching is that shown in *A. kaguaensis.* In this species, the second type (lobing) does not always remain limited in growth. Some of these produce upright cylindrical branches which are gemmiferous. The possibility that these are a result of etiolation is discounted since some of these branches revert to the prostrate broad growth form. There was no evidence of change in habitat which would induce this growth.

Gemmae: Asexual reproduction by means of gemmae occurs within the family Aneuraceae. However, the ability to produce gemmae seemed to be restricted to the genus *Riccardia.* These gemmae are two-celled elements produced endogenously in the epidermal cells of the thallus, usually in the region of the apex. The apparent absence of gemma production in the genus

Aneura has led workers to suggest that this character may be important taxonomically (Schuster, 1964). But since the production of gemmae has a limited duration in most species, it would seem that its importance as a taxonomic character is limited to classification on a negative basis. It can only be positive in identification when present.

However, gemma production has been observed in *A. kaguaensis*. These gemmae are not like the characteristic *Riccardia* gemmae, being multicellular exogenous elements, produced on stalks in the growing region of the narrow upright cylindrical branches peculiar to this species (Plate XI). The initial development is by transverse divisions followed by longitudinal divisions resulting in a club shaped element on a stalk cell. Each element is composed of 7–10 cells (Fig. 1).

Consequently, this observation lends support to the view that organs of asexual reproduction may be important taxonomically. More light may be thrown on the subject if gemma production could be induced experimentally in other species of the genus *Aneura*.

Oil Bodies: The use of oil bodies as an aid to identification and classification is being recommended by recent workers dealing with the family Aneuraceae (Mizutani and Hattori, 1957; Schuster, 1958, 1963, 1964). It is regrettable that it should be necessary to go to such extremes to find a positive character because the oil bodies can only be studied in fresh material. However, since the gametophyte provides such variable characters a thorough description of the oil bodies in a complete generic monograph may be valuable, especially in identification.

The oil bodies of only three species have been studied here (Fig. 1). Although these observations broaden the class value for the subgenus *Lobatiriccardia*, the two classes remain discrete. Hence, *A. cerebrata* fits the subgenus *Aneura*, and *A. alterniloba* var. *gigantea* and *A. athertonensis* fit the subgenus *Lobatiriccardia*.

Mycorrhizae: by extending the definition of the word mycorrhiza to include endothrophic associations with absorbing organs other than roots, we can say the the association observed in some members of the Family Aneuraceae is a mycorrhiza. Accepting this, then the classical example of a mycorrhiza in the Family is provided by *Cryptothallus*. Even so a mycorrhiza was described by Denis (1919) in chlorophyll-free saprophytic varities of *A. pinguis* some fourteen years prior to the description of *Cryptothallus mirabilis* by Malmborg (1933).

Mycorrhizae have been observed in six of the eight species studied. These mycorrhizae are of the orchid type as are those previously described for the Family. They are septate, form complex hyphal coils in the cells and are ultimately digested. They appear to enter through the rhizoids and infect the ventral internal cells leaving the epidermal cells uninfected. The hyphae pass through the cell walls and constrict when they do so (Plate XI). The extent of infection is usually limited to a region immediately dorsal to the region bearing rhizoids (Fig. 1).

The range in size of the hyphae is from the extremely fine 1–2μ in *A. rodwayi* to the more massive 4–5μ in *A. alterniloba*.

It is interesting to note that at least two species appear to be evolving towards the chlorophyll-free saprophytic condition of the subterranean *Cryptothallus*. They are *A. rodwayi* from Tasmania and *A. cerebrata* from New Guinea. Both are pale green, though still with chlorophyll, and both tend to be very deeply concave and sunken in their substrate. It is obvious that there is a tendency towards saprophytism and it would seem probable that more subterranean species will be discovered.

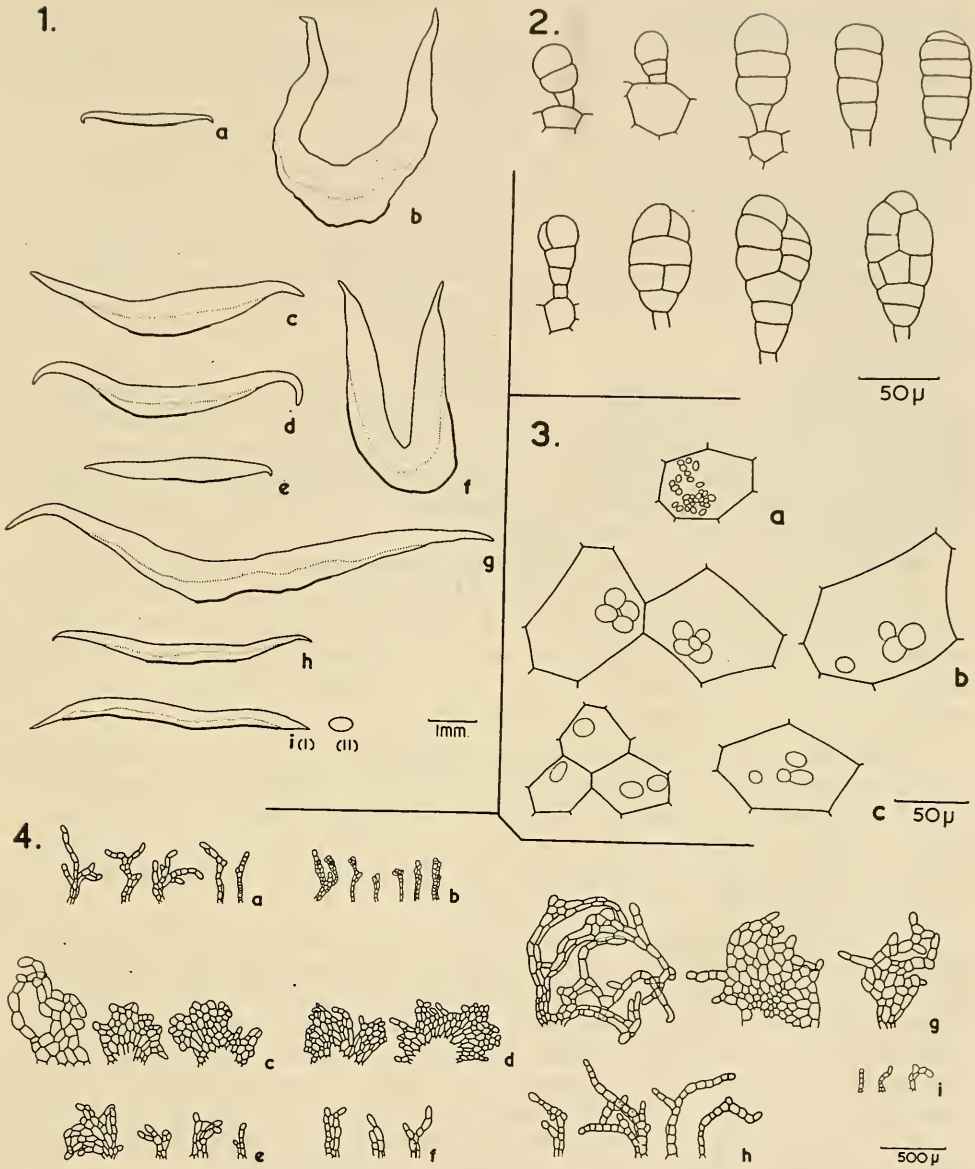


Fig. 1. 1. Transverse sections of the thallus. Mycorrhizae ventral beneath the dotted line and rhizoids in the region of the thick line. a. *Aneura eachamensis*; b. *Aneura cerebrata;* c. *Aneura alterniloba* var *gigantea*; d. *Aneura alterniloba* var *robusta;* e. *Aneura athertonesis;* f. *Aneura rodwayi;* g. *Aneura novaguineensis;* h. *Aneura giangena;* i. *Aneura kaguaensis*, (I) transverse section of prostrate thallus, (ii) transverse section or upright thallus branches.

2. Stages of development of multicellular exogenous gemmae of *Aneura kaguaensis.*

3. Oil bodies. a. *Aneura cerebrata*, in surface view; b. *Aneura alterniloba* var *gigantea*, insurface view (left), in transverse section (right); c. *Aneura athertonensis*, in surface view.

4. Pharaphyese. a. *Aneura eachamensis;* b. *Aneura cerebrata;* c. *Aneura alterniloba* var *gigantea;* d. *Aneura alterniloba* var *robusta;* e. *Aneura athertonensis;* f. *Aneura rodwayi;* g. *Aneura novaguineensis;* h. *Aneura giagena;* i. *Aneura kaguaensis.*

Sexual Reproduction: (i) Oecy—distribution of gametangia: All species examined are dioecious.

(ii) Male branches: When compared with *Riccardia,* the *Aneura* male branches are very irregular. There seems to be a tendency towards degeneration of the organization of this branch. Firstly, *A. alterniloba* and *A. athertonensis* are the only two species retaining the regular two row orientation of the antheridia. The remainder of the species bear their antheridia in irregular groups. Secondly, in *A. kaguaensis* the branch is so reduced that it appears to be lost. The antheridia are borne on the margin of the thallus or at the base of the upright cylindrical branches. Thirdly, in *A. novaguineensis* the antheridia are scarcely sunken in an antheridial chamber, but appear to be borne almost superficially. This is a result of very limited upward growth of the vegetative tissue of the branch between the antheridia.

(iii) Female branches: The female fertile regions of the thalli are lateral beneath the notch of the lobe branches. The archegonia are protected by (*a*) overtopping of the vegetative tissue of the branch, (*b*) lateral extension of the margin of the thallus and (*c*) a variety of multicellular hairs and scales. These I am calling paraphyses because some of them actually occur between the archegonia as well as around them.

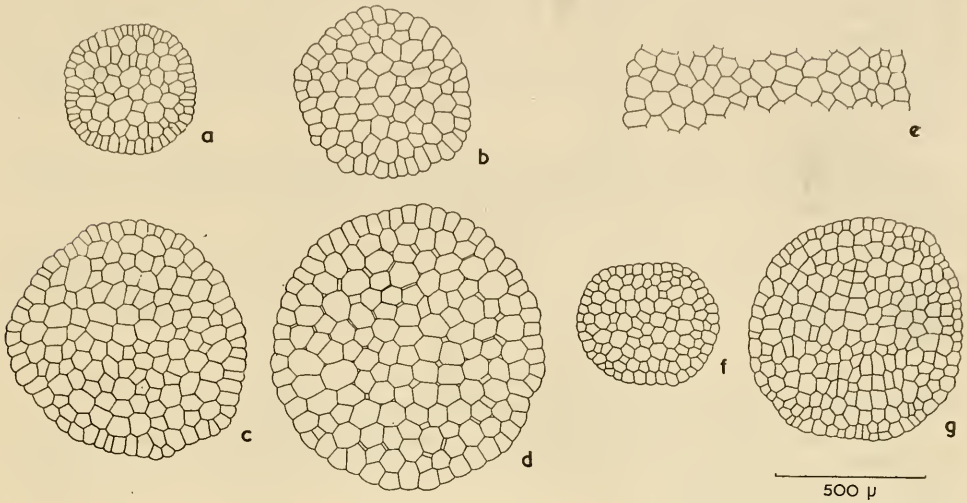
The paraphyses are essentially highly modified scales (Fig. 1). They can be divided into two groups. (*a*) Hairlike scales being 1–3 cells broad at the base. (*b*) True scales being more than 3 cells broad at the base. The hairlike scales may be (1) simple with little or no branching, (2) fimbriate, (3) flat and scalelike without fimbriation, or (4) club-shaped terminally. The true scales may be (1) dentate, or (2) fimbriate.

Calyptra: (i) Size and thickness of calyptra: The *Aneura* calyptra is usually massive when compared with the *Riccardia* calyptra. It is rarely less than 3 mm. long at maturity. However the calyptra wall is not always a massive fleshy structure. The thickness in terms of number of cells seems to be a positive character for each species. Hence the calyptra wall of *A. eachamensis* (3–4 cells) is quite delicate.

(ii) Calyptra armation: In their treatment of the Japanese *Riccardiae*, Mizutani and Hattori (1957) classify the calyptra armation into two types, the *Trichostylium*-type, and the *Riccardia*-type. The genus *Aneura* has the *Trichostylium*-type, having rhizoid-like cilia and tubercles (scaly outgrowths). However these are absent in some species. *A. eachamensis* has a smooth calyptra; *A. alterniloba* var. *robusta* has a range of variation which includes some smooth calyptrae; and *A. rodwayi* has a smooth calyptra, however in the latter species only one capsule from an herbarium specimen was examined. Hence this observation needs to be checked in the field.

Sporophyte: (i) Seta: Mizutani and Hattori (1957) use seta diameter as one of the characters separating the two subgenera. The observations here show that the distinction is not clear-cut. Accepting 12 cells in diameter as the point of difference between the two subgenera, then clearly *A. athertonensis* falls across the two classes (Fig. 2.) Putting the level down to eleven cells in diameter would be equally unsatisfactory because *A. pellioides,* which is clearly in the subgenus *Aneura* on oil body and capsule wall characters, now would be in the subgenus *Lobatiriccardia.* An attempt to solve this has been made by noting the number of cells in the circumference. Hence the classes would be subgenus *Aneura* (35–55 cells) and *Lobatiriccardia* ((50) 55–60 cells). But *A. athertonensis,* which is clearly in the subgenus

Lobatiriccardia on oil body and capsule wall characters, would have to be classified in subgenus *Ancura* on this basis. Consequently it would seem that seta size is unsatisfactory in the delimitation of the subgenera as circumscribed by Mizutani and Hattori.



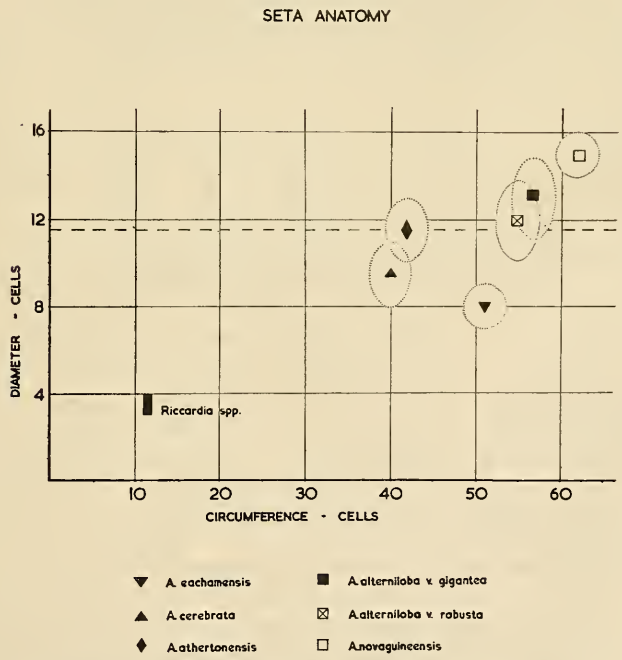


Fig. 2. Transverse sections of Setae of: a. *A. eachamensis*, b. *A. cerebrata*, c. *A. alterniloba* var *gigantea*, d. *A. alterniloba* var *robusta*, e. *A. rodwayi*, f. *A. athertonensis*, g. *A. novaguineensis;* and an analysis of Seta Anatomy for interpretation of subgenera.

(ii) Capsule wall anatomy: Evans (1937) studied the distribution of thickenings in the walls of the capsule wall cells of six species. He found two types. Mizutani and Hattori (1957) applied this study to the Japanese *Riccardiae sens. lat.* Evans' first type, which is found in the genus *Riccardia sens. str.,* they called *Riccardia*-type. Evans' second type, which is found in the genus *Aneura*, they called *Trichostylium*-type (Fig. 3). This has bands of thickenings on both adaxial and abaxial radial walls of the outer cell layer, and on the inner tangential and adaxial and abaxial radial walls (U-shaped) of the inner cell layer. This type is found in the subgenus *Aneura* (Plate XII).

They found a third type which is also found in the genus *Aneura*. This they called the *Lobatiriccardia*-type. Schuster (1964) described a variation of this and a third variation is described here.

(*a*) "Mizutani". This has bands of thickenings on the adaxial radial walls of the outer cell layer, and on the inner tangential and abaxial radial walls (L-shaped) and often on the adaxial radial walls (U-shaped) of the inner cell layer.

(*b*) "Schuster". This has the bands of the inner cell layer on the inner tangential and both the adaxial and abaxial radial walls (U-shaped).

(*c*) "Australia". This has the bands of the inner cell layer on the inner tangential and adaxial radial walls (L-shaped), and often on the abaxial radial walls (U-shaped).

These three variations are found in the subgenus *Lobatiriccardia* (Plate XII).

(iii) Spores: (*a*) Ornamentation: Spore wall ornamentation in the Bryophyta is now being described using palynological terminology (Erdtman, 1957). *Cryptothallus* spores have an areolate sexine pattern on the spore wall. This term was first used by Jackson (Kremp, 1965) and means divided into areas (areolae) separated by small grooves. However, the sexine pattern of the *Aneura* and *Riccardia* spore wall has been described as papillose or asperulate by Schuster (1964). The term asperulate does not appear to be in use in palynology. However, my interpretation of the term papillose is a pattern with projections or elevations which are small and narrow.

If we follow Harris's definition of papillate (see Kremp, 1965), then the "papilla" must not be less than 1μ in height. Moveover it is a projection and irrespective of height (above 1μ), must be less than twice as long as wide as seen in surface view. A papillate projection is a narrow one. Elevations have a length more than twice the width as seen in surface view.

On these definitions I have observed only one species which has projections. This is *A. cerebrata* (Plate XI). It has a pattern which ranges up to 1·5μ in height and is narrow. Hence it is papillate (= baculate). Occasionally some of these papillae appear to fuse to form elevations. The other species have "projections" which are less than 1μ in height. This is minutely sculptured (Harris, see Kremp, 1965) and they are scabrate, the pattern being flecked with minute "projections". However, in *A. eachamensis* these "projections" are slightly larger and pilate. They have a terminal thickening.

(*b*) Size: Mizutani and Hattori (1957) use spore diameter as one of the characters separating the two subgenera. The subgenus *Trichostylium* has spores 20–25μ in diameter, while the subgenus *Lobatiriccardia* has spores 12–16μ in diameter. Schuster (1964) supports this but extends the range for the subgenus *Lobatiriccardia* to 12–19μ in diameter. But some of the

Australian species form intermediates between the two classes and hence this character is inadequate as a basis for subgeneric classification as circumscribed by Mizutani and Hattori.

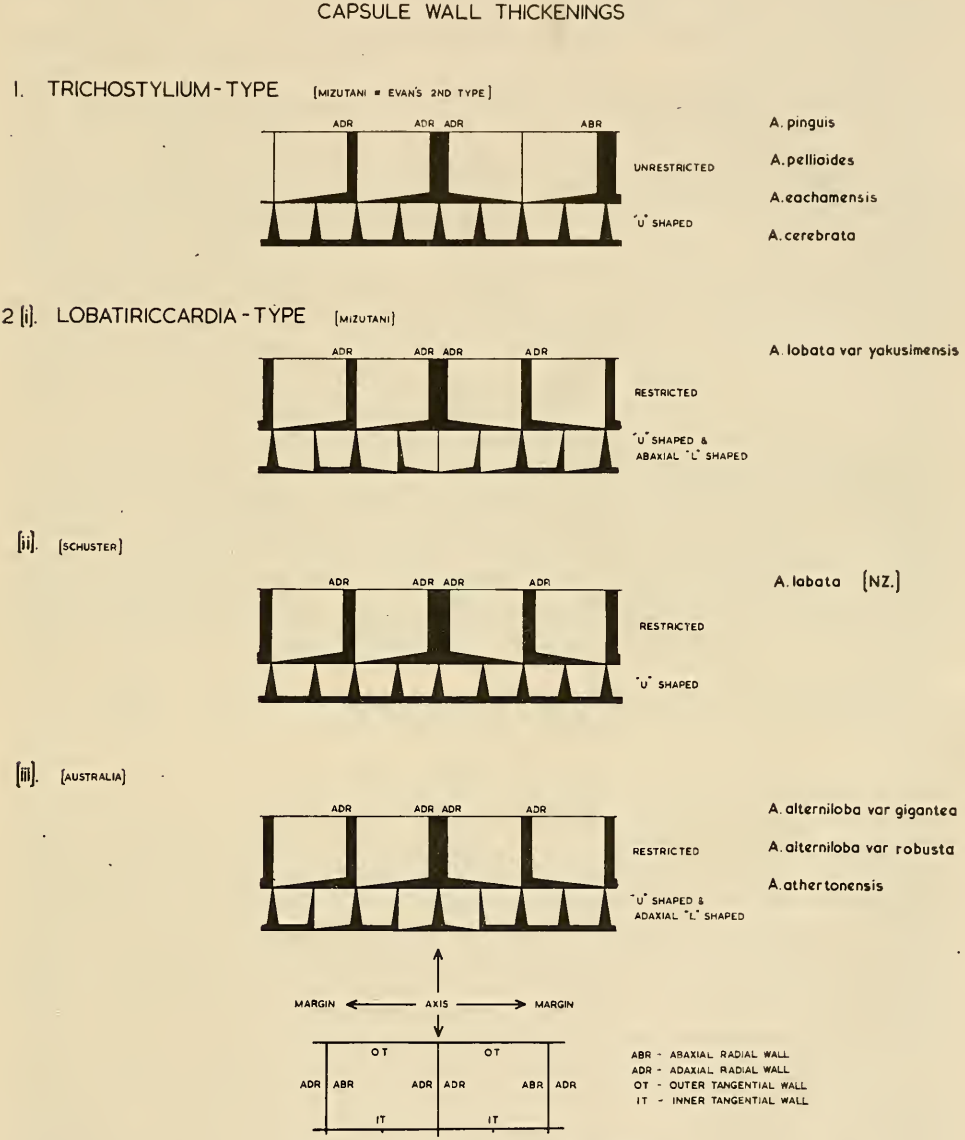


Fig. 3. Capsule wall thickenings.

Chromosomes: Counts have been made on four species. Ten was found to be the haploid number of *A. eachamensis, A. cerebrata* and *A. novaguineensis.* However *A. alterniloba* var. *gigantea* was found to have eight. There was no evidence of polyploidy in this genus. The cytology is to be dealt with in Part III of this treatment.

Distribution: The distribution is to be discussed in Part III of this treatment.

Generic Description

Aneura Dumortier, Commentationes Botanicae, 115, (1822).

Nomenclatural synonym: *Trichostylium* Corda, in Sturm, Deutschlands Flora, 2.5.6: 116, 119 (1835).

Taxonomic synonym: *Jungermannia* Linnaeus, Sp. Pl., 2: 1136 (1753) pp., excl. lectotype.

Dioecious. Plants prostrate in damp to wet habitat on rock, soil, or wood. *Thalli* waxy, yellowish to dark green, 1–8 cm. long, (1·5) 2–6 (10) mm. wide, with (rarely obtuse) acute to winged margins, ± dentate, plano- to concavo-convex (with recurved margins) to deeply concave in transverse section, (5) 7–20 (30) cells thick; branching pinnate with bipinnate lobes (rarely tripinnate lobes); apices deeply dissected; mucilage papillae ventral, non-persistent; rhizoids ventral; cuticle smooth. *Gemmae* multicellular exogenous, known in one species only. *Mycorrhizae* usually present in ventral internal cells. *Oil bodies* (fine) granular botryoidal, (1) 3–40 (70) per cell, 1·5 × 2·5–15 × 20μ. *Male plants* with lateral male branches; antheridia arranged regularly in two rows or irregularly, up to 15 antheridia per row; dorso-lateral wing up to 6 cells wide. *Female plants* with latero-ventral female branches, produced beneath lobes with thallus margin often dentate and overtopping; paraphyses hairlike to scalelike, arranged around or both around and between the archegonia. *Calyptra* massive, (2) 3–5 (10) mm. long at maturity, (3) 5–12 (15) cells thick; pachydermal ornamentation smooth or tuberculate, and/or ciliate (up to 500μ long). *Seta* 8–17 cells in diameter. *Capsule wall thickenings* of the *Trichostylium*-type, or the *Lobatiriccardia*-type. *Spores* 10–25μ in diameter, minutely sculptured with scabrate or pilate "projections", or papillate projections. *Haploid chromosome number* ten, except for *A. alterniloba* var. *gigantea* which has eight.

Typification: *Aneura* Dumortier—Lectotype—*Aneura pinguis* (L.) Dumortier (*Jungermannia pinguis* Linnaeus).

Species Descriptions

1. *Aneura eachamensis* Hewson, sp. nov.

Dioica. Thallus magnus, 1–3 cm. longus, (1·5) 2–3 (5) mm. latus, plano-convexus, (7) 9–10 (12) cellulis crassitie, margine acuto, plus minusve alato dentatoque; ramificatio irregularis, lobata. *Rami plantarum masculinarum* laterales, antheridiis in seriebus 2–4 irregularibus ordinatis, alis 1–2 (3) cellulis latitudine. *Plantae femineae* squamis pilisque multicellularibus archegonia cingentibus. *Calyptra* (2) 3 (5) mm. longis, laevis, 3–4 cellulis crassitie. *Seta* 8 cellulis diametro. *Paries capsulae* eo *Trichostylii* similis. *Sporae* 14–22μ crassae. *Chromosomata gametophytica* 10.

Dioecious. Plants prostrate on basalt rock in rain-forest. *Thalli* 1–3 cm. long, (1·5) 2–3 (5) mm. wide, with an acute ± winged margin, dentate especially in female plants, plano-convex usually with recurved margins in transverse section, (7) 9-10 (12) cells thick; branching of two types, pinnate with bipinnate lobes; apex deeply dissected and protected by ventral, non-persistent mucilage papillae; rhizoids ventral; cuticle smooth. *Gemmae* not observed. *Mycorrhizal association* not observed. *Oil bodies* unknown. *Male plants* bearing lateral antheridial branches, (1) 2–3 (5) together; antheridia in 2–4 irregular rows, up to 12 per row; dorso-lateral wing 1–2 (3) cells wide, irregular. *Female plants* bearing archegonia laterally beneath lobes; lateral margin of the thallus dentate and usually overtopping the archegonia; archegonia surrounded by multi-cellular, fimbriate, scalelike paraphyses. *Calyptra* (2) 3 (5) mm. long at maturity; smooth (in Hewson 401 a few

capsules had slightly raised epidermal cells near the apex); not massive, 3–4 cells thick. *Seta* 8 cells in diameter. *Capsule wall anatomy* of *Trichostylium*-type. *Spores* 14–22μ in diameter, minutely sculptured, pilate. *Chromosome number*: n = 10.

Typification: *Aneura cachamensis* — Holotype — Vision Falls, Lake Eacham, Atherton Tableland, on basalt rock in rain-forest, Queensland, Hewson, 398, 8.1964, (NSW): Isotype (BRI).

Specimens examined: Vision Falls, Lake Eacham, Queensland, Hewson, 396, 401, 8.1964, (SYD.BRI).

Distribution: This species has a North Queensland distribution. It was not found on Mt. Spec, the Eungella Mtns., or the Bunya Mtns. It is possible that it extends further up the Cape York Peninsula and even as far as New Guinea.

Discussion: On the basis of capsule wall anatomy this species would be placed in the subgenus *Aneura,* as circumscribed by Mizutani and Hattori. It is the only species recorded for Australia found to be in this subgenus, and has no very close affinities with the other species.

2. *Aneura cerebrata* Hewson, sp. nov.

Dioica. Thallus magnus, 1–2 (3) cm. longus, (1·5) 2–5 (10) mm. latus, crispus, fragilis, valde concavus 15–20 (30) cellulis crassitie, margine acuto; ramificatio irregularis, lobata. *Corpora oleosa* 20–30 in quaque cellula, $2 \times 3–5 \times 8\mu$. *Rami plantarum masculinarum* laterales, antheridiis in seriebus 3–4 irregularibus ordinatis, alis 1–2 cellulis latitudine. *Plantae femineae* pilis multicellularibus, claviformibus circum interque archegonia. *Calyptra* 5 mm. longis, tuberculata, 9–10 cellulis crassitie. *Seta* 10 cellulis diametro. *Paries capsulae* eo *Trichostylii* similis. *Sporae* 10–17μ crassae. *Chromosomata gametophytica* 10.

Dioecious. Plants on damp soil in dense crisp patches often appearing like a pale green brain coral. Thalli 1–2 (3) cm. long, (1·5) 2–5 (10) mm. wide, with a sub-acute to acute margin (not winged or dentate), very deeply concave, with the margins presented dorsally and closely appressed to neighbouring thalli, 15–20 (30) cells thick; branching of two types, pinnate with bipinnate lobes; apex deeply dissected and protected by ventral, non-persistent mucilage papillae; rhizoids ventral; cuticle smooth. *Gemmae* not observed. *Mycorrhizae* in ventral internal cells, hyphae 2–3μ wide. *Oil bodies* 20–30 per cell, $2 \times 3–5 \times 8\mu$ in diameter. *Chloroplasts* tend to be densely concentrated in upper region of thallus, and especially in the more exposed epidermal cells. *Male plants* bearing lateral antheridial branches, 1–3 together; antheridia in 3–4 irregular rows, up to 10 per row; dorso-lateral wing 0–2 cells wide. *Female plants* bearing archegonia laterally beneath the lobes, but presented dorsally as a result of the extreme concavity of the thallus; multicellular, club-shaped, hairlike paraphyses around and between the archegonia. *Calyptra* up to 5 mm. long at maturity, 9–10 cells thick, tuberculate at the apex. *Seta* 10 cells in diameter. *Capsule wall anatomy* of the *Trichostylium*-type. *Spores* 10–17μ in diameter, papillate. *Chromosome number*: n = 10.

Typification: Aneura cerebrata—Holotype—Chimbu River, Gembogl, 2,100 m., on granite soil on river bank, Chimbu District, New Guinea, Hewson, 577, 8.1965, (NSW): Isotype (LAE.L).

Specimens examined: New Guinea: Murigl River, Omkali, 1,370 m., Chimbu District, Hewson, 564, 7.1965, (NSW.LAE.L); Pengage Creek, Mt. Wilhelm, 2,590 m., Chimbu District, Hewson, 581, 8.1965, (NSW.LAE.L);

Lake Pinde, Mt. Wilhelm, 3,650 m., Chimbu District, Hewson, 612, 618, 8.1965, (NSW.LAE.L) ; Lake Aunde, Mt. Wilhelm, 3,500 m., Chimbu District, Hewson, 627, 8.1965, (NSW.LAE.L) ; near Brass Tarn, Mt. Wilhelm, 3,650 m., Chimbu District, Hewson, 646, 8.1965, (NSW.LAE.L).

Distribution: New Guinea.

Discussion: On the basis of capsule wall anatomy and oil body characters this species would be placed in the subgenus *Aneura* as circumscribed by Mizutani and Hattori. It has no close affinities with other species of *Aneura* described for New Guinea.

3. *Aneura alterniloba* (Hook.f. et Tayl.) Tayl., in Gottsche, Lindenberg, and Nees, Syn. Hep., 496 (1846) ; J. D. Hooker, Handbook of the New Zealand Flora, 543 (1867) ; Stephani, Sp. Hep., 1 : 270 (1899) ; Rodway in Pap. & Proc. Roy. Soc. of Tas., 1916 : 62 (1917) ; Schuster in J. Hatt. Bot. Lab., 26 : 295 (1963).

Nomenclatural synonyms: *Jungermannia alterniloba* Hook.f. et Tayl., in Lond. J. Bot., 3 : 572 (1844).

Sarcomitrium alternilobum (Hook.f. et Tayl.) Mitt., in J. D. Hooker, The Botany of the Antarctic Voyage, Flora Novae Zelandiae, 2, 2 : 167 (1855), et loc. cit., Flora Tasmaniae, 3, 2 : 239 (1860) ; Bastow in Pap. & Proc. Roy Soc. of Tas., 1887 : 275 (1888).

Riccardia alterniloba (Hook.f. et Tayl.) Trevis., in R. Ist. Lomb. Sci. Lett. Rend., 431 (1877).

Taxonomic synonym: *Aneura epibrya* Col., in Trans. Proc. N.Z. Inst., 18 : 253 (1886) ; Stephani in J. Linn. Soc. Lond., 29 : 273 (1892) ; synonymy proposed by Stephani in Sp. Hep., 1 : 270 (1899).

Misapplied name: *Aneura pinguis* (non (L.) Dum.) ∝ *lobulata, major* Gottsche, in Beitrage zur Pflanzenkunde, 28 : 560 (1856).

Dioecious. Plants grow prostrate on rock, or soil in damp to wet conditions, often in spray of water-falls, or in running water. *Thalli* (2) 3–6 (8) cm. long, (2) 3–6 (10) mm. wide, with acute ± dentate margin, usually dentate in female plants, plano- to concavo-convex with slightly to very recurved margins in transverse section, (5) 7–12 (15) cells thick; branching of two types, pinnate with bipinnate lobes which tend to be opposite; apex deeply dissected and protected by ventral, non-persistent mucilage papillae; rhizoids ventral; cuticle smooth. *Gemmae* not observed. *Mycorrhizae* in ventral internal cells, hyphae 4–5μ in diameter. *Oil bodies* (1) 2–5 (8) per cell, 3 × 3–15 × 20μ. *Male plants* bearing lateral antheridial branches, 1–3 (4) together; antheridia in 2 regular, or 2–3 irregular rows, up to 12 per row; dorso-lateral wing 2–3 cells wide. *Female plants* bearing archegonia laterally beneath lobes; lateral margin of the thallus dentate, and overtopping the archegonia; archegonia surrounded by multicellular, fimbriate, scalelike paraphyses. *Calyptra* massive, (3) 5–8 (10) mm. long, 5–12 cells thick, smooth to tuberculate or tuberculate and ciliate. *Seta* 11–15 cells in diameter. *Capsule wall anatomy* of the *Lobatiriccardia*-type (2. (iii).). *Spores* 14–21μ in diameter, minutely sculptured, scabrate. *Chromosome number*: n = 8 in the New South Wales representatives.

Distribution: New Zealand, New South Wales, Victoria, and Tasmania.

Discussion: On the basis of capsule wall anatomy and oil body characters this species would be placed in the subgenus *Lobatiriccardia* as circumscribed by Mizutani and Hattori.

Aneura alterniloba (Hook.f. et Tayl.) Tayl. var. *alterniloba* (Hook.f. et Tayl.) comb. nov. occurs in New Zealand.

Aneura alterniloba (Hook.f. et Tayl.) Tayl. var. *gigantea* (Stephani), comb. nov.

Nomenclatural synonym: *Aneura gigantea* Stephani, in J. Proc. Roy. Soc. NSW, 48: 95 (1914).

Misapplied name: *Aneura dentata* (non Steph.), Rodway in Pap. & Proc. Roy. Soc. of Tas., 1916: 63 (1917).

Thalli (2) 3–6 (8) cm. long, (2) 4–6 (8) mm. wide, (5) 7–10 (12) cells thick. *Oil bodies* (1) 2–5 (8) per cell, 5 × 8–15 × 20μ. *Male branches* with antheridia in 2–3 irregular rows. *Calyptra* (5) 8–12 cells thick, tuberculate at the apex, ± cilia, 200–300 (500)μ long (these may be present or absent from capsules even at the same locality, not to be confused with rhizoids which are often on the ventral surface of the calyptra, up to 1000μ long). *Seta* 12–15 cells in diameter. *Spores* 14–19μ in diameter. *Chromosome number*: n = 8.

Typification: *Aneura gigantea* Steph.—Holotype—Cambewarra Mtn., under cliff, Watts, 920, 10.1907, (G 11042): Isotype (920 NSW).

Specimens examined: Tasmania: Adventure Bay, Tas., sine leg., 3, 5, 3.1921, (HO); West Coast, sine leg., 4, 11.1923, (HO); New South Wales: Somersby Falls, Hewson, 847, 7.1966, (SYD); Warrah, Pearl Beach, Hewson, 145, 146, 7.1963, 158, 8.1963, (SYD); Mermaid's Glen, Blackheath, Hewson, 847, 7.1966, (1966); Neate's Glen, Blackheath, Hewson, 3, 2.1963, 76, 5.1963, 172, 8.1963, (SYD); Wentworth Falls, Hewson, 99, 5.1963, (SYD); Bilpin, Hewson, 301, 4.1964, (SYD); Oxford Falls, Sydney, Hewson, 62, 5.1963, 155, 7.1963, (SYD); East Lindfield, Hewson, 153, 7.1963, (SYD); North Shore, Whitelegge, 24, 61, 8.1884, (MEL); Flat Rock Creek, North Shore, sine leg., 22, (NSW); Waterfall, Royal National Park, Hewson, 17, 3.1963, (SYD); Oakdale, Hewson, 37, 45, 4.1963, (SYD); Fitzroy Falls, Hewson, 194, 195, 8.1963, (SYD); Charlotte's Pass, Mt. Kosciusko, Hewson, 287, 1.1964, (SYD).

Distribution: New South Wales, and Tasmania.

Aneura alterniloba (Hook.f. et Tayl.) Tayl. var. *robusta* (Rodway), comb. nov.

Nomenclatural synonym: *Aneura alterniloba* (Hook.f. et Tayl.) Tayl. f. *robusta* Rodway in Pap. & Proc. Roy. Soc. of Tas., 1916: 62 (1917).

Thalli (2) 3–5 (6) cm. long, (2) 3–6 (10) mm. wide, (6) 8–12 (15) cells thick. *Oil bodies* 1–3 per cell, 3 × 3–8 × 15μ. *Male branches* with antheridia in two regular rows. *Calyptra* 5–10 cells thick; no pachydermal armation, though some specimens tend to be tuberculate near the apex. *Seta* 11–14 cells in diameter. *Spores* 17–21μ in diameter. *Chromosomes* unknown.

Typification: *Aneura alterniloba* (Hook.f. et Tayl.) Tayl. f. *robusta* Rodway—Holotype—Russell Falls, Mt. Field National Park, Tas., in wet places, Rodway, sine No., 11.1914, (HO ex Herb. Rodway).

Specimens examined: Tasmania: St. Patrick's River, sine leg., 1769 (NY ex Herb. W. Mitten); Russell Falls, Mt. Field National Park, Townrow, 150, 151, 7.1963, Hewson, 254, 9.1963, (SYD); Arve Bridge, Mt. Hartz National Park, Hewson, 225, 9.1963, (SYD); Reid's Track, Mt. Wellington, Hewson, 264, 9.1963, (SYD); Victoria: Sealer's Cove, Gottsche (MEL); Sealer's Cove, Wilson's Promontory, F. Mueller, 5.1853, (MEL); Loutit Bay, Lorne, Otways. Luehmann, (MEL); Ryson's Creek, Nth. of Labertouche, Willis, 56W, (MEL); Calder River, Sth. Otway Ranges, Wakefield, 44W, (MEL); Nayook Reserve, nr. Neerim Junction, Warragul Field Naturalists, 77W, (MEL).

Distribution: Victoria and Tasmania.

Discussion: In view of the absence of cilia on the calyptra in this taxon it is possible that it should be recognized as a new species. But the range of variation in *A. alterniloba* var. *gigantea* includes some capsules without cilia. However, there are positive variations in other characters, and if the haploid chromosome number of var. *robusta* is found to be ten, it should probably be accepted as a separate species.

4. *Aneura athertonesis* Hewson, sp. nov.

Dioica. Thallus magnus, 2–3 (5) cm. longus, 2–4 mm. latus, plano-convexus (7) 8–10 (12) cellulis crassitie, margine acuto, alato ramificatio irregularis, lobata. *Corpora oleosa* 1–3 (4) in quaque cellula 8 × 15–10 × 18μ. *Rami plantarum masculinarum* laterales, antheridiis in seriebus duabus regularibus ordinatis, alis 1–2 cellulis latitudine. *Plantae femineae* squamis pilisque multicellularibus archegonia cingentibus. *Calyptra* 4–6 mm. longis, ciliata, 4–6 cellulis crassitie. *Seta* 11–12 cellulis diametro. *Paries capsulae* eo *Lobatiriccardiae* similis. *Sporae* 10–15μ crassae.

Dioecious. Plants on basalt rock with other bryophytes on creek banks in disturbed rainforest. *Thalli* 2–3 (5) cm. long, 2–4 mm. wide, with an acute ± dentate margin, plano-convex usually with recurved margins in transverse section, (7) 8–10 (12) cells thick; two types of branching, pinnate with bipinnate lobes; apex deeply dissected and protected by ventral, non-persistent mucilage papillae; rhizoids ventral. *Cuticle* smooth. *Gemmae* not observed. *Mycorrhizal association* not observed. *Oil bodies* 1–3 (4) per cell, 8 × 15–10 × 18μ in diameter. *Male plants* bearing lateral antheridial branches, 1–3 together; antheridia in two regular rows, up to 5 per row; dorso-lateral wing 1–2 cells wide. *Female plants* bearing archegonia laterally beneath lobes; margin of thallus usually overtops the branch; archegonia surrounded by multicellular, fimbriate, scalelike paraphyses. *Calyptra* 4–6 mm. long at maturity, 4–6 cells thick, ciliate with pachydermal cilia up to 400μ long. *Seta* 11–12 cells in diameter. *Capsule wall anatomy* of the *Lobatiriccardia*-type. *Spores* 10–15μ in diameter, minutely sculptured, scabrate. *Chromosomes* unknown.

Typification: *Aneura athertonensis*—Holotype—Charmillan Creek, Tully Falls Road, Atherton Tableland, on basalt rock on creek bank in disturbed rain-forest, Qld., Hewson, 422, 8.1964, (NSW) : Isotype (BRI).

Specimens examined: Charmillan Creek, Atherton Tableland, Qld., Hewson, 425, 8.1964 (SYD.BRI).

Distribution: North Queensland.

Discussion: On the basis of capsule wall anatomy and oil body characters this species would be placed in the subgenus *Lobatiriccardia* as circumscribed by Mizutani and Hattori. It is close to *A. alterniloba* but differs in having smaller seta, smaller spores, less massive calyptra, smaller paraphyses, and no mycorrhizal association.

5. *Aneura rodwayi* Hewson, sp. nov.

Misapplied names: *Sarcomitrium pinguis* (non (L.) Mitten), Bastow in Pap. & Proc. Roy. Soc. of Tas., 1887: 276 (1888).

Aneura pinguis (non (L.) Dum.), Rodway in Pap. & Proc. Roy. Soc. of Tas., 1916: 62 (1917).

Dioica. Thallus magnus, (1) 2–3 (4) cm. longus, (2) 3–5 (10) mm. latus, concavus, 10–20 (25) cellulis crassitie, margine acuto; ramificatio irregularis, lobata. *Rami plantarum masculinarum* laterales, antheridiis in seriebus irregularibus ordinatis, alis 2–3 cellulis latitudine. *Plantae femineae* squamis pilisque multicellularibus archegonia cingentibus. *Calyptra* laevis, 10–15 cellulis crassitie. *Seta* 13–15 cellulis diametro.

Dioecious. Plants pale green, usually in dense patches on clay soil. *Thallus* (1) 2–3 (4) cm. long, (2) 3–5 (10) mm. wide, with an acute to winged, ± dentate margin, concave- to deeply concave-convex with margins appressed, giving appearance of a brain coral which is buried almost to the level of the substrate, 10–20 (25) cells thick; branching of two types, pinnate with bipinnate lobes; apex deeply dissected and protected by ventral, non-persistent mucilage papillae; rhizoids ventral; cuticle smooth. *Gemmae* not observed. *Mycorrhizal association* in the ventral internal cells, hyphae 1–2μ in diameter. *Oil bodies* unknown. *Male plants* bearing lateral antheridial branches; up to 10 antheridia arranged irregularly; dorso-lateral wing 2–3 cells wide. *Female plants* bearing archegonia laterally in lobe with margin of thallus extended laterally around it; archegonia surrounded by multicellular, fimbriate, scale-like paraphyses. *Calyptra* 4+ mm. long 10–15 cells thick, without pachydermal armation, but Rodway (1917), described tubercles. *Seta* 13–15 cells in diameter. Material too immature to describe *capsule wall* and *spore* anatomy. *Chromosomes* unknown.

Typification: *Aneura rodwayi*—Holotype—Hartz River, Mt. Hartz National Park, on clay soil near river bank, Tas., Hewson, 215, 9.1963, (NSW).

Specimens examined: Tasmania Rd. to Esperance Lake, Mt. Hartz National Park, Hewson, 233, 9.1963, (SYD); Lake Dobson, Mt. Mawson, Hewson, 236, 9.1963, (SYD); Mt. Wellington, 1,330 m., Rodway, 15, 1913, (HO).

Distribution: Tasmania.

Discussion: Similar in external morphology to *A. cerebrata,* but paraphyses scalelike and surrounding the archegonia, and seta 13–15 cells in diameter. Without capsule wall anatomy and oil bodies it is difficult to classify this species. However, seta diameter indicates that it might belong to the subgenus *Lobatiriccardia,* but this character has been shown to be an inadequate basis for this classification and hence we are not justified in placing it.

6. *Aneura novaguineensis* Hewson, sp. nov.

Dioica. Thallus magnus, (1) 2–4 (5) cm. longus, (1·5) 3–5 (12) mm. latus, plano-concavus, (7) 1–15 (20) cellulis crassitie, margine acuto, plus minusve alato, plus minusve dentatoque; ramificatio irregularis, lobata. *Rami plantarum masculinarum* laterales, antheridiis superficialis, in seriebus 2–4 irregularibus ordinatis, alis 3–6 cellulis latitudine. *Plantae femineae* squamis pilisque multicellularibus archegonia cingentibus. *Calyptra* tubercularis, 12–15 cellulis crassitie. *Seta* 16 cellulis diametro. *Chromosomata gametophytica* 10.

Dioecious. Plants on damp soil with other Bryophytes in rainforest and marginal rainforest. *Thalli* (1) 2–4 (5) cm. long, (1·5) 3–5 (12) mm. wide, with an acute ± winged, ± dentate margin, plano- to concavo-convex with a tendency to recurved margins in transverse section, (7) 10–15 (20) cells thick; branching of two types, pinnate with tripinnate lobes (rarely bipinnate with tripinnate lobes); apex deeply dissected and protected by ventral, non-persistent mucilage papillae; rhizoids ventral; cuticle smooth. *Gemmae* not observed. *Mycorrhizal association* in the ventral internal cells, hyphae 3–4μ in diameter. *Oil bodies* unknown. *Male plants* bearing lateral antheridial branches, 1–4 together; antheridia superficial, in 2–4 irregular rows, up to 15 per row; dorso-lateral wing irregular, wavy, dentate, 3 to 6 cells wide. *Female plants* bearing archegonia laterally beneath lobes; margin of thallus usually continued lateral to archegonia, rarely overtopping; archegonia surrounded by multicellular, fimbriate, scalelike paraphyses. *Calyptra* 2+ mm.

long, 12–15 cells thick, with terminal tubercles. *Seta* 16 cells in diameter. *Capsule walls* and *spores* too immature for study. *Chromosome number*: n = 10.

Typification: *Aneura novaguineensis*—Holotype—track to Bulldog Road from Edie Creek, 2,130 m., on soil in rainforest, Morobe District, New Guinea, Hewson, 838, 9.1965, (NSW) : Isotypes (LAE.L).

Specimens examined: New Guinea: Chimbu River, Gembogl, Chimbu District, 2,130 m., Hewson, 573, 8.1965, (NSW.LAE) ; Pengage Creek, Mt. Wilhelm, Chimbu District, 2,780 m., Hewson, 673, 675, 8.1965, (NSW.LAE.L) ; Wakaru Range, Kagua, SHD, 1,820 m., Hewson, 695, 701, 706, 9.1965, (NSW.LAE.L) ; near Mungeri Village, Kagua, SHD., 1,670 m., Hewson, 725, 9.1965, (NSW.LAE.L) ; near Edie Creek, 2,130 m., Morobe District, Hewson, 840, 9.1965, (NSW.LAE.L).

Distribution: New Guinea.

Discussion: This species has closest affinities with *A. giangena* but differs from it in sex branch characters.

7. *Aneura giangena* Hewson, sp. nov.

Dioica. Thallus magnus, 2–3 cm. longus, 2–6 mm. latus, planus vel concavo-convexus, 8–12 cellulis crassitie, margine acuto, alato, dentato; ramificatio irregularis, lobata. *Rami plantarum masculinarum* laterales, antheridiis in seriebus duabus regularibus ordinatis, alis 2–4 cellulis latitudine. *Rami feminei* pilis multicellularibus circum interque archegonia.

Dioecious. Plants on damp soil loosely with other bryophytes in marginal rainforest. *Thalli* 2–3 cm. long, 2–6 mm. wide, with an acute, winged, dentate margin, plano- to concavo-convex with a tendency to recurved margins in transverse section, 8–12 cells thick; branching of two types, pinnate with bipinnate lobes; apex deeply dissected and protected by ventral, non-persistent mucilage papillae; rhizoids ventral; cuticle smooth. *Gemmae* not observed. *Mycorrhizal association* in ventral internal cells, hyphae 3–4μ wide. *Oil bodies* unknown. *Male plants* bearing lateral antheridial branches, 2–4 together; antheridia in 2 $\pm$ irregular rows, up to 8 per row; dorso-lateral wing 2–4 cells wide, irregular, dentate. *Female plants* bearing archegonia laterally in lobes, overtopped by thallus margin; archegonia protected by multicellular, hairlike paraphyses, around and between the archegonia. *Sporophytes* and *chromosomes* unknown.

Typification: *Aneura giangena*—Holotype—in Pengage Valley above Komamamambuno Mt. Wilhelm, 2,730 m., with other bryophytes on creek bank, in marginal rainforest, Chimbu District, New Guinea, Hewson, 668, 8.1965, (NSW) : Isotypes (LAE.L).

Distribution: New Guinea.

Discussion: It is unfortunate that sporophyte material was unavailable with this collection. The unique female branches made it worthy of description, although it shows some affinities with *A. maxima* (Schffn.) Steph. The name chosen is derived from the Chimbu word "giangen". "Giangen" is the name given to all Lichens and Bryophytes.

8. *Aneura kaguaensis* Hewson, sp. nov.

Dioica. Thallus magnus, 1–3 cm. longus, (0·5) 2–4 mm. latus, planus, 7–10 cellulis crassitie, margine acuto; ramificatio irregularis, lobata; pinnulae erectae, angustae, usque ad 1 cm. longae, 0·3–0·7 mm. latae, ellipticocirculares. *Gemmae* exogenae, multicellulares, in apicibus pinnularum dispositae. *Rami plantarum masculinarum* irregulares marginales vel in basibus pinnularum. *Plantae femineae* circum interque archegoniis, pilis multicellularibus instructis.

Dioecious. Plants prostrate on logs in disturbed rainforest. *Main thalli* 1–3 cm. long, 2–4 mm. wide, with acute margins in transverse section, 7–10 cells thick; apex not deeply dissected, protected by ventral, non-persistent mucilage papillae; rhizoids ventral; cuticle smooth. *Pinnules* up to 1 cm. long, (0·3) 0·5 (0·7) mm. wide with obtuse margins, elliptical to cylindrical in transverse section, 7–10 cells thick. *Gemmae* terminal on pinnules, multicellular, exogenous. *Mycorrhizal association* in ventral internal cells, hyphae 2–3μ in diameter. *Oil bodies* unknown. *Male branches* bearing up to 6 antheridia marginal on thallus and basal on pinnules. *Female plants* bearing archegonia laterally beneath lobes; lateral margin not overtopping branch; archegonia protected by multicellular, hairlike paraphyses, around and between archegonia. *Sporophytes* and *chromosomes* unknown.

Typification: *Aneura kaguaensis*—Holotype—track between Kagua Mungeri Village, 1,540 m., on log in disturbed rainforest, SHD, New Guinea, Hewson, 720, 8.1965, (NSW): Isotypes (LAE.L).

Distribution: New Guinea.

Discussion: This species has three types of branching, pinnate with bipinnate lobes or bipinnate upright cylindrical pinnules. The lobing is typical of *Aneura* and the pinnules appear as though the plant has suffered etiolation. There was no apparent cause of etiolation in the field, but it was noted that some of the narrow branches reverted to normal broad thalli which in turn produced more cylindrical branches. Consequently it is inferred that this habit is usual rather than abnormal.

It is unfortunate that sporophyte material was unavailable with this collection. However the unique method of asexual reproduction appears to distinguish it clearly from all other species, and may ultimately lead to the establishment of a new genus.

Key to the Australian Species of Aneura

1. Calyptra delicate, 3–4 cells thick; seta less than 10 cells diameter; capsule wall with bands of thickenings on either ad. or abaxial walls in the outer row of cells, and on the inner tangential and both ad. and abaxial walls on the inner row of cells; mature spores with minutely sculptured sexine pattern, pilate; oil bodies 5–70/cell, less than 5μ in diameter. ..... *A. eachamensis*

1+. Calyptra massive, more than 4 cells thick; seta more than 10 cells diameter; capsule wall with bands of thickenings on the adaxial walls in the outer row of cells, and on the inner tangential, the adaxial and often the abaxial walls in the inner row of cells; mature spores with minutely sculptured sexine pattern, scabrate; oil bodies 1–12/cell, 5–20μ in diameter. 2

2. Calyptra 4–6 cells thick; seta 11–12 cells in diameter, 39–45 cells in circumference. (N. Qld.). ..... *A. athertonensis*

2+. Calyptra (5) 8–10 (12) cells thick; seta 11–15 cells in diameter, 50–60 cells in circumference 3

3. Thallus 10–20 (25) cells thick, usually very deeply concave; mycorrhizal hyphae 1–2μ in diameter; archegonial paraphyses hairlike, flat to simple to slightly fimbriate, less than 0·5 mm. long ..... *A. rodwayi*

3+. Thallus (5) 7–12 (15) cells thick, plano- to slightly concavo-convex with recurved margins; mycorrhizal hyphae 4–5μ in diameter; archegonial paraphyses true scales, dentate to fimbriate, (0·4) 0·5–1·0 mm. long 4

4. Calyptra 8–12 cells thick, tuberculate and usually ciliate, cilia 200–300 (500)μ long; spores 14–19μ in diameter; oil bodies (1) 3–6 (8)/cell, 6 × 8–15 × 20μ ..... *A. alterniloba* var. *gigantea*

4+. Calyptra 5–10 cells thick, smooth to slightly tuberculate; spores 17–22μ in diameter; oil bodies 1–3/cell, 3 × 3–8 × 15μ .... *A. alterniloba* var. *robusta*

Key to Aneura *Material Lacking Sporophytes for New Guinea*

1. Thallus 7–10 cells thick, usually with two forms of growth-habit, flat prostrate and cylindrical upright; multicellular exogenous gemmae in the apical region of the upright branches; male branches reduced to lateral region on thallus or at base of upright branches; archegonial paraphyses hairlike, simple, 0·1–0·4 mm. long .... *A. kaguaensis*

1+. Thallus (7) 8–20 (30) cells thick, one form of growth-habit; without multicellular exogenous gemmae; male branches distinct lateral branch; archegonial paraphyses if hairlike are greater than 0·4 mm. long, or are club shaped 2

2. Thallus 15–20 (30) cells thick, usually very deeply concave-convex and closely appressed to resemble brain coral; mycorrhizal hyphae 2–3μ in diameter; dorso-lateral wing of male branch 1–2 cells wide; archegonial paraphyses, hairlike, club shaped, 0·2–0·5 mm. long ..... *A. cerebrata*

2+. Thallus (7) 8–15 (20) cells thick plano- to slightly concavo-convex with recurved margins; mycorrhizal hyphae 3–4μ in diameter; dorso-lateral wing of male branch 2–4 cells wide; archegonial paraphyses greater than 0·5 mm. long 3

3. Male branches with 2–4 irregular rows of antheridia up to 15 per branch, superficial, dorso-lateral wing 3–6 cells wide; archegonial paraphyses true scales, slightly to very fimbriate, 0·8–2·0 mm. long, around archegonia ..... *A. novaguineensis*

3+. Male branches 2 more or less irregular rows of antheridia up to 8 per branch, sunken, dorso-lateral wing 2–4 cells wide; archegonial paraphyses hairlike, simple to fimbriate, 0·5–1·0 mm. long, around and between the archegonia ..... *A. giangena*

References

Bastow, R. A., 1888.—Tasmanian Hepaticae. *Pap. & Proc. roy. Soc. Tasmania*, 1887: 209–289.

Bonner, C. E. B., 1962.—"Index Hepaticarum". Vol. 2. (Weinheim.)

Carrington, B., 1869.—Dr. Gray's arrangement of the Hepaticae. *Trans. & Proc. Bot. Soc. Edinburgh*, 10: 305–309.

Cavers, F., 1910–11.—*The Inter-relationships of the Bryophyta.* New Phytologist reprint, No. 4. Cambridge. (*New Phytologist*, 9: 81–112, 196–234, 231–253, 269–304; 10: 1–46, 84–86 (1910–11).)

Corda, A. K. J., 1835.—Deutschlands Jungermannien, in J. Sturm, "Deutschlands Flora." 2 (5/6): 116–121.

Denis, M. M., 1919.—Sur quelques thalles d'*Aneura* depourvus de chlorophylle. *C. R. Acad. Sci. Paris*, 168: 64–66.

Dumortier, B. C., 1822.—*Commentationes Botanicae.* Tournay.

————, 1831.—*Sylloge Jungermannidcarum Europae indigenarum.* Tournay.

Erdtman, G., 1957.—"Pollen and Spore Morphology/Plant Taxonomy. II." (Uppsala.)

Evans, A. W., 1938.—The structure of the capsule wall in certain species of *Riccardia*. *Ann. Bryol.*, 10 (1937): 20–35.

Gottsche, K. M., 1856.—Plantae Müllerianae: Hepaticae Australasiae a Dr. F. V. Müller. Linnaea. *Beitr. zur Pflanz.*, 28: 547.

————, 1867.—De Mexikanske Levermooser. *Dansk. Vid. Selsk. Skrift.*, 5, 6: 97–381.

————, Lindenberg, J. B. W., and Nees ab Esenbeck, C. G., 1844–47.—"Synopsis Hepaticarum." (Hamburg.)

Gray, S. F., 1821.—"A natural arrangement of British plants. V. 1." (London.)

Grolle, R., 1960.—Bryological Notes: Zur Nomenklatur von *Riccardia pinguis*. *Trans. Brit. bryol. Soc.*, 3 (5): 746–747.

Harley, J. L., 1959.—"The biology of mycorrhizae." (London.)

Hooker, J. D., 1867.—"Handbook of the New Zealand Flora, 2, Hepaticae." (London.)

————, and Taylor, T., 1844.—Hepaticae Antarcticae. *Lond. J. Bot.*, 3: 366–400.

Kremp, G. O. W., 1965.—"Morphologic Encyclopedia of Palynology." (Tuscon.)

Linnaeus, C., 1753.—"Species Plantarum." V. 2. (Holmiae.)

Mitten, W., 1855.—In J. D. Hooker, "Botany of the Antarctic Voyage. Flora Novae Zelandiae." V. 2. Pt. 2. (London.)

————, 1860.—In J. D. Hooker, "Botany of the Antarctic Voyage. Flora Tasmaniae." V. 3. Pt. 2. (London.)

Mizutani, M., and Hattori, S., 1957.—An etude on the systematics of Japanese *Riccardias*. *J. Hatt. Bot. Lab.*, 18: 27–64.

Nees ab Esenbeck, C. G., 1838.—"Naturgeschichte der Europäischen Lebermoose." 3: 1–594.

Rayner, M. C., 1927.—Mycorrhiza. *New Phytologist*, 26 (1): 22–45.

Rodway, L., 1917.—"Tasmanian Bryophyta." V. 2. (Hobart.) Reprinted from *Pap. & Proc. roy. Soc. Tasmania*, 1916: 1–92.

Schiffner, V., 1893.—Hepaticae, in Engler, E., and Prantl, K., "Die Natürlichen Pflanzenfamilien." 1 (3): 1–141. (Leipzig.)

Schuster, R. M., 1958.—Keys to the Orders, Families and Genera of Hepaticae of America and North of Mexico. *The Bryologist*, 61: 1–66.

————, 1963.—Studies on Antipodal Hepaticae, 1. Annotated keys to the genera of Antipodal Hepaticae with species reference to New Zealand and Tasmania. *J. Hatt. Bot. Lab.*, 26: 185–309.

————, 1964.—Studies on Antipodal Hepaticae, 4. Metzgeriales. *J. Hatt. Bot. Lab.*, 27: 183–216.

Schwägrichen, C. F., 1814.—"Historiae Muscorum Hepaticarum. Prodromus." (Leipzig.)
Stephani, F., 1892.—A revision of Colenso's Hepaticae with descriptions of new Species collected by him. *J. Linn. Soc. London*, 29: 263–280.
————, 1898–1899.—"Species Hepaticarum". V. 1. (Geneva.)
Trevisan de Saint Leon, V., 1874.—Nuovo censo delle Epatiche Italiane. *R. Ist. Lombardo di Sci. e Lett. Milano*, 2 (7): 776–786.
————, 1877.—Schema di Una Nuova Classificazione Delle Epatiche Italiane. *R. Ist. Lombardo di Sci. e Lett. Milano*, 3 (4): 383–451.

EXPLANATION OF PLATES

Plate xi

Fig. 1. Longitudinal section through a gemmiferous branch of *Aneura kaguaensis* showing developing exogenous gemmae and ventral mucilage papillae. × 100. Fig. 2. Isolated gemma of *A. kaguaensis*. × c.525. Fig. 3. Mycorrhizal hyphae released by sectioning from a cell of *Aneura cerebrata*. Note septum. × c.1310. Fig. 4. Mycorrhizal hypha in rhizoid of *Aneura rodwayi*. × c.1310. Fig. 5. Mycorrhizal hypha passing through cell wall of *Aneura alterniloba* var. *gigantea*. × c.1310. Fig. 6. Spores of *Aneura eachamensis*. Surface (left) and transverse section (right). × c.1310. Fig. 7. Spores of *Aneura cerebrata*. Surface (left) and transverse section (right). × c. 1310. Fig. 8. Spores of *Aneura alterniloba* var *gigantea*. Surface (left) and transverse section (right). × c.1310. Fig. 9. Spores of *Aneura alterniloba* var *robusta*. Surface (left) and transverse section (right). × c.1310.

Plate xii

Fig. 1. Capsule wall thickenings of *Aneura eachamensis*. Tranverse section (left), surface view of outer row of cells, (centre), surface view of inner row of cells (right). × c.282. Fig. 2. Capsule wall thickenings of *Aneura cerebrata*. Surface view of outer row of cells (left), surface view of inner row of cells (right). × c.282. Fig. 3. Capsule wall thickenings of *Aneura alterniloba* var *gigantea*. Transverse section (left), surface view of inner row of cells (centre), surface view of outer row of cells (right). × c.282. Fig. 4. Capsule wall thickenings of *Aneura alterniloba* var *robusta*. Transverse section (left), surface view of inner row of cells (centre), surface view of outer row of cells (right). × c.282 Fig. 5. Capsule wall thickenings of *Aneura athertonensis*. Surface view of outer row of cells (left), surface view of inner row of cells (right). × c.282.

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